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Response of *Sphagnum* species mixtures to increased temperature and nitrogen availability

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Abstract To predict the role of ombrotrophic bogs as carbon sinks in the future, it is crucial to understand how *Sphagnum* vegetation in bogs will respond to global change. We performed a greenhouse experiment to study the effects of two temperature treatments (17.5 and 21.7°C) and two N addition treatments (0 and 4 g N m^{-2} $year^{-1}$) on the growth of four *Sphagnum* species from three geographically interspersed regions: *S. fuscum*, *S. balticum* (northern and central Sweden), *S. magellanicum* and *S. cuspidatum* (southern Sweden). We studied the growth and cover change in four combinations of these *Sphagnum* species during two growing seasons. *Sphagnum* height increment and production were affected negatively by high temperature and high N addition. However, the northern species were more affected by temperature, while the southern species were more affected by N addition. High temperature depressed the cover of the 'wet' species, *S. balticum* and *S. cuspidatum*. Nitrogen concentrations increased with high N addition. N:P and N:K ratios indicated P-limited growth in all treatments and co-limitation of P and K in the high N treatments. In the second year of the experiment, several containers suffered from a severe fungal infection, particularly affecting the 'wet' species and the high N treatment. Our findings suggest that global change can have negative consequences for the production of *Sphagnum* species in bogs, with important implications for the carbon sequestration in these ecosystems.

Keywords Climate change · Fungal infection · Nitrogen deposition · Ombrotrophic bog · Production · Species cover · *Sphagnum* · Temperature

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Introduction

Ombrotrophic bogs are peat-forming systems and as such they can serve as important long-term sinks for atmospheric CO_2 (Gorham 1991; Rydin and Jeglum 2006). There is much concern on how global change will affect the ability of peatlands to sequester carbon and what the feedbacks to climate will be (Bragazza et al. 2006; Bubier et al. 2007; Franzén 2006). Global change encompasses changes in temperature, precipitation and nutrient deposition, especially at northern latitudes (Christensen et al. 2007) where the majority of peat bogs occur (Gunnarsson 2005). Predictions

about future precipitation patterns show great variability, but all models predict an increase in temperature and nitrogen (N) deposition (Bouwman et al. 2002; Christensen et al. 2007).

The large carbon sequestration capacity of bogs can be ascribed to the unique characteristics of *Sphagnum* (peat moss) species, which dominate the vegetation of ombrotrophic bogs. This vegetation is not uniform but differs in the different microhabitats that exist within a bog and are a result of ranges in height above the water table, pH and nutrient gradients (Andrus 1986; Limpens et al. 2003; Sjörs and Gunnarsson 2002). It has been shown that there can be remarkable differences in production (Asada et al. 2003; Gerdol 1995; Gunnarsson 2005) and in decomposition rate (Belyea 1996; Breeuwer et al. 2008b; Limpens and Berendse 2003b) between different *Sphagnum* species. The location and size of the different microhabitats and the related species composition of the *Sphagnum* layer are not stable but are the result of continuous competition between species and changing environmental variables. The composition of the vegetation also determines the characteristics of a peat bog. We have already found different responses in biomass production among species when temperature is increased (Breeuwer et al. 2008a; Robroek et al. 2007b). It seems likely that when a species with high production and/or a low decomposition rate increases its relative abundance in a bog, this will increase the carbon storage capacity of the system.

In general, climate warming is expected to increase *Sphagnum* productivity, as long as water does not become limiting (Breeuwer et al. 2008a; Dorrepaal et al. 2006; Gunnarsson 2005). The effect of increased N availability is less straight-forward because a small increase in N can enhance *Sphagnum* production at locations where N is a limiting nutrient (Turunen et al. 2004). However, when N concentrations exceed a critical threshold value, *Sphagnum* production and cover are reduced (Berendse et al. 2001; Gerdol et al. 2007; Gunnarsson and Rydin 2000; Lamers et al. 2000). Yet any positive effect of increased temperature and N on carbon sequestration in bogs may be counteracted by the positive effect of temperature (Hobbie 1996) and N (Franzén 2006) on decomposition rates. A change in temperature influences not only the production and decomposition of individual *Sphagnum* species but also the competitive balance that exists between species. Therefore, we have chosen not to examine monocultures in this study but use mixtures of two co-occurring species.

Although the effects of temperature (Asada et al. 2003; Dorrepaal et al. 2003; Gerdol 1995) and N (Aerts et al. 2001; Gerdol et al. 2007; Limpens and Berendse 2003a) on growth of different *Sphagnum* species have been studied, and a few studies have examined their separate effects on mixtures of *Sphagnum* species (Breeuwer et al. 2008a; Gunnarsson and Rydin 2000; Robroek et al. 2007a), only one study (Wiedermann et al. 2007) has examined the combined effects of temperature and N on *Sphagnum* cover. Since global warming can indirectly cause increased nutrient availability through increased decomposition and N mineralisation in bogs (Hobbie 1996; Rustad et al. 2001), it is even more important to study the effects of increased temperature and N availability together in order to predict the effect of global change on *Sphagnum* vegetation. To our knowledge, this is the first study that examines the combined effects of increased temperature and N availability on the growth of different *Sphagnum* species.

The changes in temperature, precipitation and N deposition as a result of global change are expected to differ between and within different regions in the world, including northern Europe (Christensen et al. 2007). Bogs in different climatic regions within Europe also differ in species composition and dominant *Sphagnum* species. Therefore, global change impacts may differ among ombrotrophic bogs over northern Europe. In our study, we used *Sphagnum* species from three different sites in Sweden situated over a north–south gradient. At the sites in northern and central Sweden, *Sphagnum balticum* (Russ.) C. Jens. and *Sphagnum fuscum* (Schimp) H. Klinggr are the dominant species. At the site in southern Sweden these species also occur, but *Sphagnum magellanicum* (Brid.) and *Sphagnum cuspidatum* (Hoffm.) are the most abundant species. This corresponds with the general distribution of these species in Europe, since both *S. magellanicum* and *S. cuspidatum* occur further south than *S. fuscum* and *S. balticum* (Daniels and Eddy 1985).

To examine the effect of temperature and N on the performance of *Sphagnum* species, we performed a greenhouse experiment in which we studied the effect of two temperature treatments and two N treatments on the growth of four species originating from three

sites: *S. fuscum* and *S. balticum* from the northern and central Swedish site and *S. magellanicum* and *S. cuspidatum* from the southern Swedish site. Four combinations of species were made to study the effects of temperature and nitrogen addition on *Sphagnum* growth. We examined how the different *Sphagnum* species from different sites of origin respond to increased temperature and N availability and whether both species in a mixture show the same response. If one species profits more from increased temperature or N availability, it will increase in cover. Since *S. fuscum* and *S. magellanicum* grow in drier and therefore also warmer microhabitats than *S. balticum* and *S. cuspidatum*, we expected them to be better adapted to higher temperatures. *S. magellanicum* grows in more southerly sites than *S. balticum*, so we expected this species to be better adapted to higher temperatures. Consequently, we hypothesised (1) that all four species will show increased growth with increased temperature, (2) that hummock and southern species will respond with larger height increment, biomass production and cover than hollow and northern species, (3) that high temperature will increase N uptake by *Sphagnum* due to increased N mineralisation and (4) as N concentration in the *Sphagnum* increase (from N addition and increased mineralisation) the growth of all *Sphagnum* species will decline.

Materials and methods

Plant material

In August 2003, *Sphagnum* cores (diameter 22–23 cm, height 16 cm) were collected at three different sites in Sweden, situated along a latitudinal gradient of ca. 800 km. All sites were relatively undisturbed, with a peat layer of at least 5 m deep and vegetation characteristic of ombrotrophic mires. At the northern site Lappmyran (N-Sweden, 64°09′ N, 19°35′ E), we collected 10 *S. fuscum* and 10 *S. balticum* cores. Lappmyran is a string flark mire with ridges of hummocks and hollows where *S. fuscum* is dominant on the hummocks and *S. balticum* in the drier parts of the hollows. The mean temperature in July is 14.7°C (Alexandersson et al. 1991); mean annual precipitation is 652 mm (Swedish Meteorological and Hydrological Institute, SMHI) and mean annual N deposition is about 0.3 g m^{-2} (Tarrasón et al. 2006). When identifying the species from this site in the lab, we found specimens of both *S. balticum* and *Sphagnum angustifolium* (Russ.) C. Jens. These species are difficult to distinguish, as Russow (Smith 1978) and Klinggraff (Daniels and Eddy 1985) found: they identified both species as varieties of *S. recurvum*. In our samples, we were unable to quantify the exact percentages of *S. balticum* and *S. angustifolium*. When reporting the results, therefore, whenever we mention *S. balticum* from this site, we are referring to a mixture of *S. balticum* and *S. angustifolium*.

At the central Swedish site Åkerlänna Römosse (C-Sweden, 60°01′ N, 17°22′ E), we collected 10 *S. fuscum* and 20 *S. balticum* cores. Here, the peatland surface shows a typical microtopography of hollows, lawns and hummocks. *S. fuscum* is the dominant species on the hummocks and *S. balticum* in the hollows and lawns. The mean temperature in July is 16.4°C (SMHI); mean annual precipitation is 563 mm (SMHI) and mean annual N deposition is about 0.6 g m^{-2} (Tarrasón et al. 2006).

At the southernmost site Saxnäs Mosse (S-Sweden, 56°51′ N, 13°27′ E), we collected 20 *S. magellanicum* and 10 *S. cuspidatum* cores. At this site *S. magellanicum* is the dominant species on the lawns and low hummocks, while *S. cuspidatum* dominates in the hollows and pools. The mean temperature in July is 17.0°C (Malmer et al. 2003); mean annual precipitation is 1,199 mm (SMHI) and mean annual N deposition is about 1.1 g m^{-2} (Tarrasón et al. 2006).

Cores were taken from monospecific stands of each *Sphagnum* species (>95%) with sparse vascular plant cover (<5%). The cores were placed in plastic containers (diameter 22.3 cm, height 16.2 cm). Vascular plants were clipped flush with the *Sphagnum*, and other *Sphagnum* species were removed with tweezers. The containers were brought to Wageningen and stored outside until March 2004, in order to acclimatise.

Experimental design

In March 2004, the containers were brought into the greenhouse and randomly divided over the treatments and five replicate blocks, with four species combinations, two temperature treatments (T1: 17.5°C and T2: 21.7°C) and two levels of N supply (N1: no N addition and N2: application of 4 g N m^{-2} $year^{-1}$)

Table 1 Treatment codes and characteristics

Treatment code	Temperature (°C)		Rel. humidity (%)		VPD		N (g m^{-2} year$^{-1)}$
	Day	Night	Day	Night	Day	Night	
T1N1	18.4	15.7	78	84	0.47	0.29	0
T1N2	18.4	15.7	78	84	0.47	0.29	4
T2N1	22.6	20.1	71	73	0.80	0.64	0
T2N2	22.6	20.1	71	73	0.80	0.64	4

Rel. humidity relative humidity, *VPD* vapour pressure deficit, *N* nitrogen

Values for temperature, Rel. humidity and VPD are day-time (16 h) and night-time (8 h) means

per block (Table 1). The following four species combinations were made: two combinations of two northern species, *S. fuscum* with *S. balticum* from N-Sweden (combination 1) and C-Sweden (combination 2); one combination of two southern species, *S. magellanicum* with *S. cuspidatum* from S-Sweden (combination 3), and one combination of a northern with a southern species: *S. balticum* from C-Sweden with *S. magellanicum* from S-Sweden (combination 4). To study the relative performance of a northern and a southern species, we opted for the combination of *S. balticum* and *S. magellanicum* because they occur at similar water levels. To make the combinations, the cores were cut into four quarters. Next, two quarters of each of the two species in the combination were placed alternately in an empty container. When potting the species combinations, we made certain that the surface of the mixture was uniform.

The experiment was conducted in two adjacent climate-controlled greenhouse compartments from April 2004 until November 2005. Between November 2004 and April 2005, the mesocosms overwintered outside underneath a transparent roof, because it was not possible to maintain low temperatures in the greenhouse. In total, the containers were in the greenhouse for 372 days. Each greenhouse compartment was assigned one of two temperature treatments. Treatments and containers were switched between compartments every 2 weeks to minimise any effect of the different compartments. The position of the blocks and the position of containers within the blocks were also switched every 2 weeks. The average day temperatures in the two temperature treatments T1 and T2 were 18.4 and 22.6°C, respectively (Table 1). During the dark period of 8 h, the temperature was lowered by approximately 2.5–15.7 and 20.1°C, resulting in mean daily temperatures in T1 and T2 of 17.5 and 21.7°C, respectively. If light intensity was low during the 16-h light period, SON-T AGRO 400 (Philips Powertone 400) lamps supplemented the natural light. Relative humidity during the day was set at 75%. In the greenhouse it was not possible to keep the relative humidity exactly the same with both temperatures. The rise in temperature between treatments corresponded with a decrease in relative humidity, which caused an additional increase in vapour pressure deficit (VPD) with increased temperature (Table 1). Even if the relative humidity had been equal in both compartments, the VPD would still have been 1.3 times higher at T2 than at T1. Our highest VPD of 0.80 kPa with a temperature of 22.6°C is actually still low compared to field conditions (Dorrepaal et al. 2003; Hobbie and Chapin 1998).

Each year, 4 g N m^{-2} was added to the containers in the N2 treatment. This amount of N was equally distributed over 15 applications in 2004 and 11 applications in 2005 (ca. every 2 weeks) by watering with 200 ml of NH_4NO_3 solution. The N1 containers received the same amount of demineralised water. These applications preceded the addition of water to top up the water table to the desired level.

The water level was set to 1 cm below capitula at the start of the experiment. All species were subjected to the same water level, so that temperature was the only changing environmental variable. This relatively high water level was used for all species combinations because hollow species cannot grow at low water levels, while hummock species can cope with the environmental conditions of hollows quite well; nonetheless, hummock species are absent from the hollows because the hollow species are stronger competitors (Rydin and McDonald 1985). Grosvernier et al. (1997) found that growth in height and dry weight is equal for *S. fuscum* grown at water levels of

1 and 40 cm below moss surface, while for *S. magellanicum* and even more so for *S. fallax,* growth in height and dry weight is much greater at the high water level. During the experiment an artificial rainwater solution, an 8,000-fold dilution of a seawater solution (Garrels and Christ 1965), was added twice a week to top up the water level to 1 cm below capitula. In a number of containers, *Sphagnum* grew higher than 1 cm above the container so to keep the water level at 1 cm below the moss surface; the height of the container was extended by gluing a plastic rim on the containers and waterproofing the join with silicone sealant.

Measurements

Height increment of the *Sphagnum* carpet was measured non-destructively every month using a variation of the cranked wire method (Clymo 1970; Limpens et al. 2003). One cranked wire was inserted in each quarter of the mixtures. The rods, which had a diameter of 1.5 mm, did not seem to interfere with the growth of the surrounding *Sphagna*. For height increment per species, we only used measurements from cranked wires around which the original *Sphagnum* species occupied at least 15% of the surface, this excluded 14 out of 320 cranked wires.

We calculated biomass production by multiplying height increment over the total experimental period by bulk density at the end of the experiment. We did not use data on biomass production per species because it was impossible to calculate bulk density per species, since at the end of the experiment the species were no longer confined to their original quarters and all sub-samples contained a mixture of both species. This method was used because there was no relation between the bulk density and the species cover around the cranked wire. Furthermore, in monocultures used in another greenhouse experiment at approximately the same temperature treatments (Breeuwer et al. 2008a), we found no differences in bulk density between the species in the combinations that we used in this experiment. To determine bulk density at the end of the experiment, columns with a diameter of 5 cm were cut around each cranked wire and cut off at 5 cm length, after which each column was put in a plastic Ziplock bag. All columns were stored at 1°C until further measurements could be taken. Capitula (0–1 cm) and subcapitula (1–3 cm) were separated per column and oven dried at 70°C for at least 48 h and then weighed. Capitulum and subcapitulum dry weight were used to calculate bulk density and biomass production, to account for changes in capitulum density. The biomass production during the experiment per unit area (g m^{-2}) was calculated as follows:

$$\text{height increment (m)} \times \text{final bulk density [cap + subcap]} \left(\text{g m}^{-3}\right)$$

For nutrient analyses, samples of capitula were pooled per species for each container. Total N, P and K concentrations were determined by digesting 300 mg of homogeneous, milled material with sulphuric acid, salicylic acid, selenium and hydrogen peroxide. All samples were analysed spectrophotometrically for total N and P, using an auto-analyser (Skalar). K concentrations were measured with an atomic absorption spectrophotometer (Varian AAS). To compare nutrient concentrations with initial values, we collected five samples from monocultures of the four *Sphagnum* species from the containers before they were put in the greenhouse in March 2004. Measurements of nutrient concentrations were conducted as described above.

To measure the change in cover of the species in the mixtures, digital images were made at the start and end of the experiment. From these images, we measured the total surface cover per species in each pot, using Image J (1.33u, National Institute of Health, USA). At the end of the experiment, the *Sphagnum* in 37 containers was necrotic, possibly as a result of a fungal infection with *Lyophyllum palustre* (Limpens et al. 2003). Fruiting bodies similar to those of *L. palustre* appeared in several containers, but no molecular analysis was done to confirm the fungus species. The total percentage of dead *Sphagnum* was calculated from the digital images.

Data analysis

The data were tested for normality and equality of variance. When necessary, data were ln-transformed to achieve homogeneous variances. Block effect was tested as random factor. When no block effect was detected, which was usually the case, block was omitted from the analysis to gain extra degrees of freedom. All analyses were conducted using the SPSS statistical package for Windows (15.0).

Height increment was first analysed with RM-ANOVA, with year as within-subject factor, and species combination, T, N and species as between-subject factors. Since interaction effects appeared of year × species combination, year × N, year × species, year × combination × T × species and combination × species, we then analysed height increment with RM-ANOVA per species combination. Because there were significant interaction effects between year and species, we further analysed the effect of T and N per species and year with ANOVA.

The change in cover of 'wet' species was analysed with RM-ANOVA, with year as within-subject factor, T, N and combination as between-subject factors and percentage necrosis as a covariate. Since there was no significant effect of percentage necrosis, the analysis was repeated without covariate.

Biomass production was analysed with ANOVA, with T, N and combination as fixed factors. We further analysed the effect of T and N per combination.

N concentration, N:P ratio, N:K ratio and *Sphagnum* necrosis were analysed with ANOVA, with combination, T and N as fixed factors. Percentage necrosis was further analysed with separate ANOVAs per combination with T and N as independent factors. Nitrogen concentration was further analysed with separate ANOVAs per combination with T, N and species as independent factors. Because there were significant interaction effects for species × N treatment, we further analysed the effect of T and N on N concentration per species. For multiple comparisons, Tukey's a posteriori test was used. We examined the relation between N concentration and percentage necrosis with linear regression analysis.

Results

Height increment in *Sphagnum*

With one exception, in all combinations there was a negative effect of both high temperature and high N addition on height increment; the exception was the containers from S-Sweden, which only showed a negative effect of high N addition (Table 2). There were no significant interactions between temperature and N, except for a trend in the combination of *S. balticum* from C-Sweden and *S. magellanicum* from S-Sweden.

When the effects of temperature and N addition were analysed per species and year, there were different responses to the treatments (Fig. 1). In year 1 we found negative effects of high temperature on *S. balticum* from N-Sweden (Fig. 1a) and negative effects of high N addition on the height increment of *S. cuspidatum* (Fig. 1e) and *S. magellanicum* (Fig. 1f) in containers from S-Sweden. In year 2, the height increment of all species was negatively affected by high N addition, except for height increment of *S. cuspidatum* and *S. magellanicum* in combination 3, which showed no treatment effects (Fig. 1e, f). In addition, the height increments of *S. fuscum* from N-Sweden and of *S. fuscum* and *S. balticum* in the containers from C-Sweden were also negatively affected by high temperature (Fig. 1b–d).

Species cover

As there were no significant effects of species combination or interaction with species combination on cover change, we pooled the cover change of *S. balticum* and *S. cuspidatum,* which are the 'wet' species in the combinations since their natural habitat is closer to the water table than the habitat of *S. fuscum* and *S. magellanicum*. In the first year, *S. balticum* and *S. cuspidatum* increased their cover at the expense of *S. fuscum* and *S. magellanicum* in all treatments (Fig. 2). In the second year, their cover decreased in all treatments (within-subject effect of year: $F = 135.608$, $P < 0.001$). Particularly, high temperature had a negative effect on 'wet' species cover (between-subject effects of T: $F = 6.644$, $P = 0.012$; N: $F = 1.229$, $P = 0.272$; T × N: $F = 0.185$, $P = 0.669$).

Production per container

Sphagnum production over all combinations was affected negatively by high temperature ($F = 17.865$, $P < 0.001$) and high N addition ($F = 17.209$, $P < 0.001$). There was no difference in production between combinations ($F = 0.431$, $P = 0.731$) and there were no significant interactions between T, N and combination. Production decreased in the combinations in the following order: T1N1, T1N2, T2N1 and T2N2, being 1695 ± 132, 1139 ± 139, 1129 ± 107 and 624 ± 121 g m^{-2}, respectively.

When the effects of temperature and N addition were analysed per combination, we found different

Table 2 Results of RM-ANOVA for height increment per combination

Source	df	Combination 1 bal + fus N-S		Combination 2 bal + fus C-S		Combination 3 cus + mag S-S		Combination 4 bal N-S + mag S-S	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subjects									
T	1	5.906	**0.021**	12.526	**0.001**	0.071	0.791	6.865	**0.013**
N	1	11.366	**0.002**	8.981	**0.005**	10.614	**0.003**	19.703	**<0.001**
Species	1	3.201	0.083	1.896	0.178	0.120	0.732	1.203	0.281
T × N	1	0.163	0.689	0.685	0.414	0.234	0.632	3.439	0.073
T × species	1	1.202	0.281	0.002	0.969	0.388	0.538	0.162	0.690
N × species	1	0.031	0.862	0.290	0.594	0.001	0.977	0.392	0.536
T × N × species	1	0.096	0.758	0.819	0.372	0.017	0.899	0.126	0.725
Within subjects									
Year	1	19.468	**<0.001**	27.628	**<0.001**	9.018	**0.005**	1.426	0.241
Year × T	1	5.106	**0.031**	1.378	0.249	1.832	0.185	0.430	0.517
Year × N	1	0.515	0.478	1.588	0.217	0.025	0.874	5.907	**0.021**
Year × species	1	3.700	0.063	1.661	0.207	0.072	0.790	9.672	**0.004**
Year × T × N	1	1.567	0.220	0.075	0.787	0.512	0.480	0.146	0.705
Year × T × species	1	24.318	**<0.001**	0.051	0.823	0.111	0.742	0.088	0.768
Year × N × species	1	0.001	0.976	1.333	0.257	0.058	0.811	1.540	0.224
Year × T × N × species	1	6.346	**0.017**	0.151	0.701	0.449	0.508	0.621	0.436

Numbers in bold indicate significant values ($P \leq 0.05$)

T temperature treatment, *N* nitrogen treatment (for description, see Table 1); Bal *S. balticum*, fus *S. fuscum*, cus *S. cuspidatum*, mag *S. magellanicum*, *N-S* north Sweden, *C-S* central Sweden, *S-S* south Sweden

responses to the treatments (Fig. 3). Production in containers of *S. fuscum* and *S. balticum* showed a negative effect of high temperature (N-Sweden: $F = 4.393$, $P = 0.052$ and C-Sweden: $F = 8.601$, $P = 0.010$). In containers from S-Sweden, production was affected negatively by N addition ($F = 5.714$, $P = 0.029$). Production in containers of *S. balticum* from C-Sweden and *S. magellanicum* from S-Sweden was affected negatively both by high temperature ($F = 9.273$, $P = 0.008$) and by N addition ($F = 6.216$, $P = 0.024$).

Nitrogen concentration

N concentrations were higher in the high temperature treatment ($F = 5.590$, $P = 0.019$) and the high N treatment ($F = 99.659$, $P < 0.001$). The N concentration differed between combinations ($F = 6.189$, $P = 0.001$), being higher in combinations 2 (C-Sweden) and 4 (*S. balticum* from C-Sweden with *S. magellanicum* from S-Sweden) than in combination 3 (S-Sweden). The N concentration in combination 1 (N-Sweden) had intermediate values. There were no significant interactions between T, N and combination.

N addition increased the N concentration of all species, except for *S. balticum* from C-Sweden (Fig. 4). High temperature also increased the N concentration of *S. fuscum* in the absence of N addition (N1) (Fig. 4). *S. balticum* and *S. fuscum* from N-Sweden had the lowest initial values: 7.9 and 9.1 mg g^{-1}, respectively. Nitrogen concentration increased most in *S. fuscum* from N-Sweden with high temperature and high N addition, reaching a concentration of 23.2 mg g^{-1}.

N:P ratios were high in all containers, ranging between 25 and 53 at the start of the experiment to 35–86 at the end of the experiment (data not shown). N:P ratios were higher in the high N treatment ($F = 80.999$, $P < 0.001$) and differed between combinations ($F = 3.726$, $P = 0.013$), although Tukey's a posteriori test did not separate different subsets.

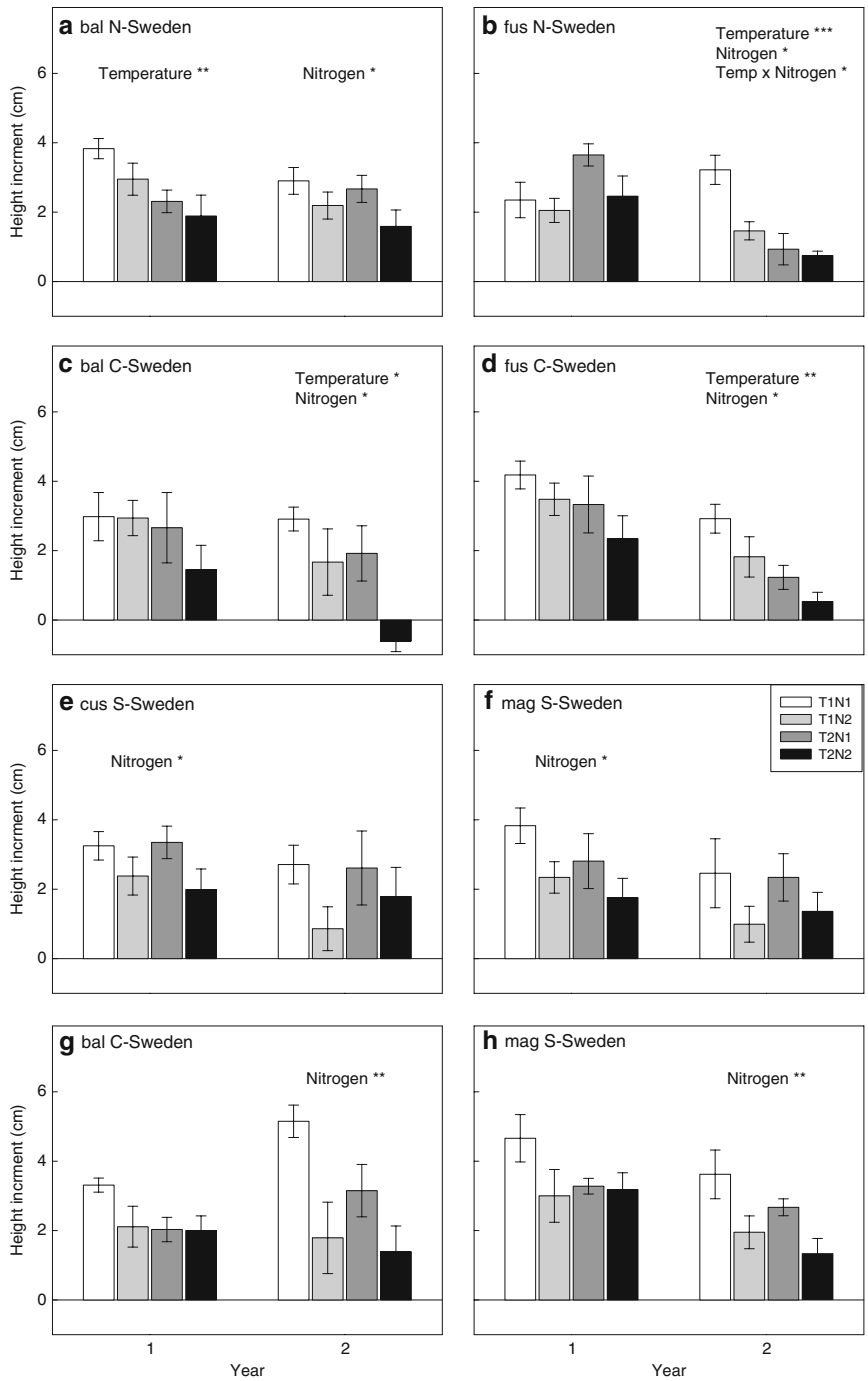


Fig. 1 *Sphagnum* species height increment during the first and second period in the greenhouse. Combination 1: **a** *S. balticum* and **b** *S. fuscum* from N-Sweden. Combination 2: **c** *S. balticum* and **d** *S. fuscum* from C-Sweden. Combination 3: **e** *S. cuspidatum* and **f** *S. magellanicum* from S-Sweden. Combination 4: **g** *S. balticum* from C-Sweden and **h** *S. magellanicum* from S-Sweden. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Data are mean values ± SE, $n = 5$. For treatment codes see Table 1

N:K ratios were high in all containers, ranging between 1.7 and 3.8 at the start of the experiment to 1.6–5.1 at the end of the experiment (data not shown). N:K ratios were higher in the high N treatment ($F = 120.329$, $P < 0.001$) and differed between combinations ($F = 5.232$, $P = 0.002$), being highest in containers from N-Sweden and C-Sweden and lowest in containers from S-Sweden; N:K ratios in containers with combination 4 had intermediate values.

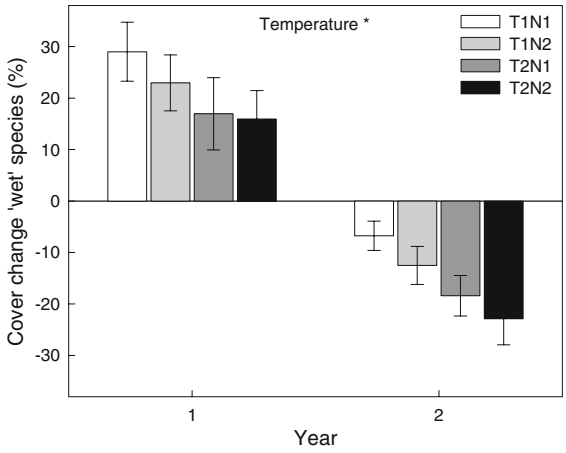


Fig. 2 Change in cover of *S. balticum* and *S. cuspidatum*. Year 1: cover change between 23-03-2004 and 19-10-2004. Year 2: cover change between 19-10-2004 and 3-11-2005. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$. Data are mean values ± SE, $n = 20$. For treatment codes see Table 1

Sphagnum necrosis

There were significant differences between sites (effect of combination: $F = 4.401$, $P = 0.007$) in the percentage of *Sphagnum* that suffered from necrosis due to fungal infection. The percentage necrosis was lowest in containers with *S. balticum* and *S. fuscum* from N-Sweden (Fig. 5). Nitrogen addition increased the percentage necrosis in both temperature treatments (effect of N: $F = 23.232$, $P < 0.001$). Increased temperature also lead to increased necrosis in the containers with *S. balticum* and *S. fuscum* from C-Sweden (Fig. 5). In all containers that suffered from necrosis, a greater proportion of the 'wet' *Sphagnum* species were affected compared with the 'dry' species (personal observation).

We found a positive relationship between N concentration and percentage necrosis ($P = 0.013$), but the relationship is very weak ($R^2 = 0.040$). When the regression analysis is split per species combination, the R^2 values are of the same order of magnitude, but models are not significant.

Discussion

To our knowledge, this is the first study on the combined effects of both increased temperature and N deposition on the growth of different *Sphagnum* species. Our findings suggest that high temperature and N addition both have a negative effect on

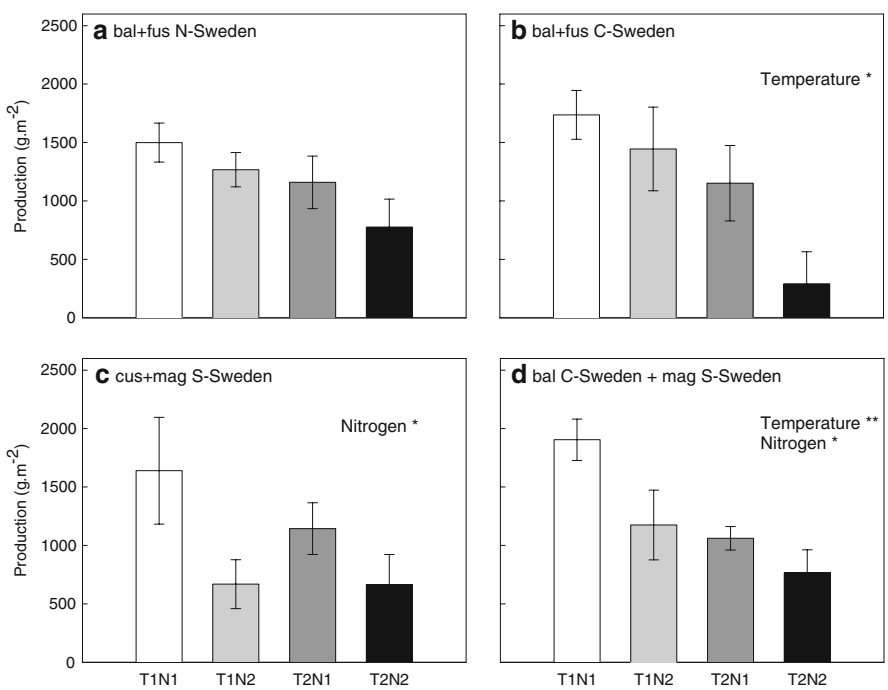
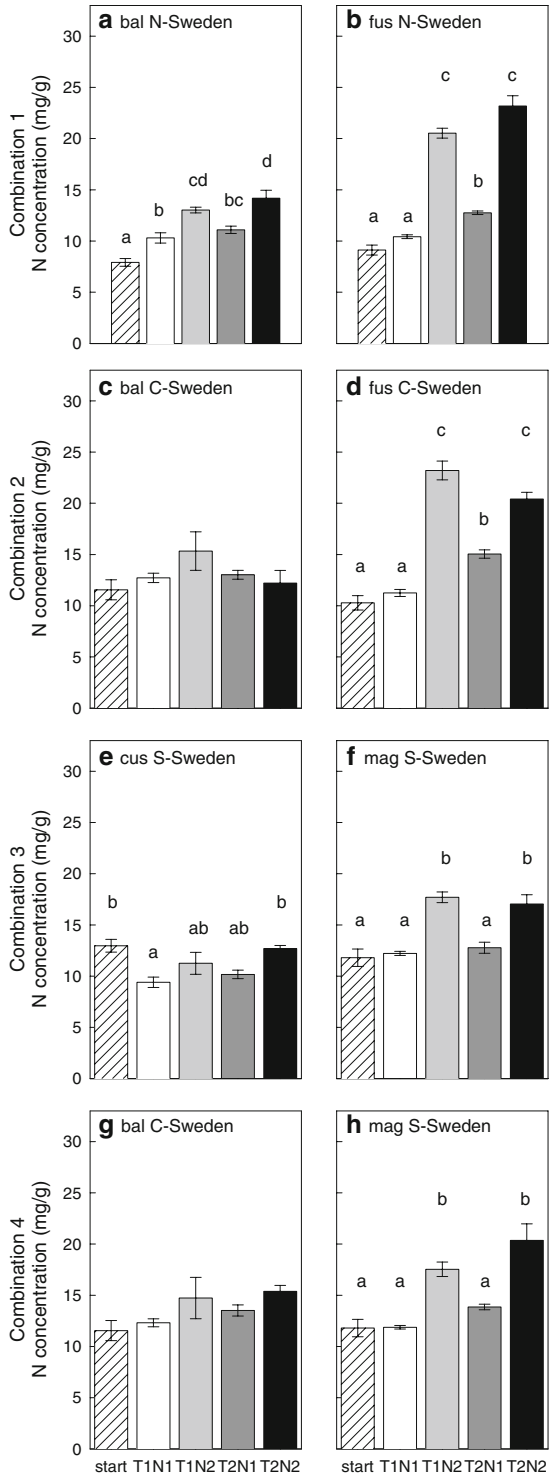


Fig. 3 Total *Sphagnum* production over 2 years per treatment (see Table 1) for each species combination. **a** Combination 1: *S. balticum* + *S. fuscum* from N-Sweden. **b** Combination 2: *S. balticum* + *S. fuscum* from C-Sweden. **c** Combination 3: *S. cuspidatum* + *S. magellanicum* from S-Sweden. **d** Combination 4: *S. balticum* from C-Sweden + *S. magellanicum* from S-Sweden. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$, ** $P < 0.01$. Data are mean values ± SE, $n = 5$



◀ **Fig. 4** Nitrogen concentrations in capitula of **a** *S. balticum* and **b** *S. fuscum* from N-Sweden in combination 1; **c** *S. balticum* and **d** *S. fuscum* from C-Sweden in combination 2; **e** *S. cuspidatum* and **f** *S. magellanicum* from S-Sweden in combination 3; **g** *S. balticum* from C-Sweden and **h** *S. magellanicum* from S-Sweden in combination 4. *Different letters* indicate significant differences between treatments ($P < 0.05$). Data are mean values ± SE, $n = 5$. For treatment codes see Table 1

Sphagnum growth. However, these effects differ between species and between the sites where the species were collected.

Temperature

Contrary to our first hypothesis, increased temperature did not have a positive effect on *Sphagnum* growth. Other studies have shown that increased temperature can increase *Sphagnum* production (Asada et al. 2003; Dorrepaal et al. 2003; Gerdol 1995), but the temperatures used in those experiments were lower and varied between 8 and 15°C. Though Robroek et al. (2007b) did find greater height increment and production at 20°C than at 15°C for several *Sphagnum* species, their experiment lasted for only 6 months. Harley et al. (1989) and Skre and Oechel (1981) showed that photosynthesis in *Sphagnum* increases with temperature up to an optimum around 20–25°C. The absence of a response to temperature in our experiment may indicate that the maximum photosynthetic rates of *Sphagnum* were already reached at the average temperatures of 17.4 and 21.7°C we used. In another greenhouse experiment, we found an increase in height increment and production when temperature increased from 10.6 to 17.2°C, but there was no difference in height increment and production between temperatures of 17.2 and 20.6°C (Breeuwer et al. 2008a). That experiment lasted only one growing season and had no N addition, so the results should be comparable to values of the T1N1 and T2N1 treatments in the first year. This proved to be the case, including the small positive effect of high temperature on height increment of *S. fuscum*.

Negative effects of increased temperature have been found in other studies too (Gerdol et al. 2007; Weltzin et al. 2001) but have usually been ascribed to desiccation. In our experiment desiccation could not have been the cause of the negative effect of temperature, because we saw no desiccated capitula. Moreover, the VPD of 0.80 kPa with a temperature of 22.6°C is low compared to field conditions. We calculated VPD from mean day temperature and

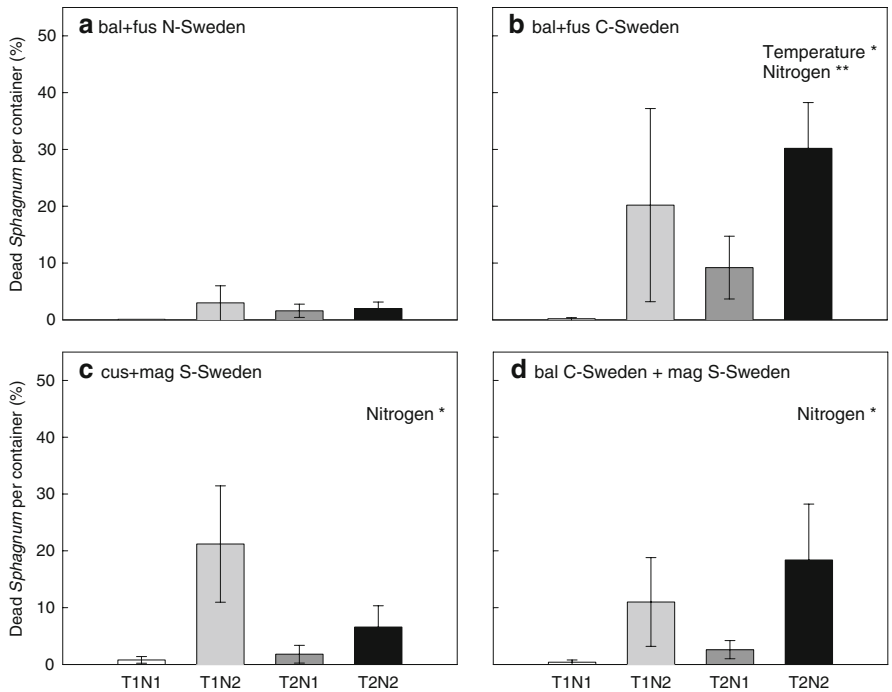


Fig. 5 Percentage dead *Sphagnum* per container at the end of the experiment. Significant effects of the temperature and N treatments are indicated: * $P < 0.05$, ** $P < 0.01$. Data are mean values ± SE, $n = 5$. For treatment codes see Table 1; for description of combinations, see Fig. 3

relative humidity in June and July in the three sites of origin of the *Sphagnum* material used in this experiment: at temperatures ranging from 6.5 to 23.7°C, the VPD ranged from 0.04 to 1.84 kPa. These values are in the same range as found in earlier studies (Dorrepaal et al. 2003; Hobbie and Chapin 1998).

In accordance with our second hypothesis, the height increment of northern species was depressed more by increased temperature than the height increment of southern species. Recent climate change simulation models with the A1B scenario for northern Europe in the year 2099 compared with the year 1999 predict an increase of 2.7°C (min–max: 1.4–5.0°C) in summer temperature, an increase of 4.3°C (min–max: 2.6–8.2°C) in winter temperature and more precipitation in northern Scandinavia (Christensen et al. 2007). For the species from the northern site, the temperature treatments simulated an average to very high increase in summer temperature (N-Sweden: T1: +2.8°C, T2: +7.0°C). For the species from the central and southern Swedish sites, the temperature treatments simulated a small to large increase in temperature (C-Sweden: T1: +1.1°C, T2: +5.3°C; S-Sweden: T1: +0.5°C, T2: +4.7°C). Although the relative increase in temperature was therefore higher for *S. fuscum* and *S. balticum* from the northernmost site than for these species from the central site, their height increment and production did not differ between containers from these sites. Apparently, there is no clear effect of local adaptation to temperature within the northern species. In contrast, there did seem to be a difference between the northern and the southern species, since the height increment and biomass production of *S. balticum* and *S. fuscum* responded negatively to high temperature, while *S. cuspidatum* and *S. magellanicum* showed no response to temperature.

Though there was no difference between height increment in the 'dry' and 'wet' species within containers, the finding that cover of 'wet' species declined in response to high temperature does support our hypothesis, because, all other things being equal, wet habitats are also colder than dry habitats (Rydin and Jeglum 2006). The increase in cover of the 'wet' species *S. balticum* and *S. cuspidatum* in the first year is not unexpected, as the water level we used was relatively high and in the range of the natural habitat of these species. These results correspond to the findings from a field experiment of Rydin (1986) and the greenhouse experiment mentioned above (Breeuwer et al. 2008a). The decrease in cover of the 'wet' species in the second year might be related to the percentage necrosis which mainly affected the 'wet' species, but when percentage necrosis was tested as a

covariate, there was no significant effect of percentage necrosis on cover change. Percentage necrosis was not affected significantly by temperature, but there was a trend for increased necrosis with high temperature in combinations with *S. balticum* from C-Sweden.

Our third hypothesis posited that the release of nutrients, and therefore the resulting N concentrations in *Sphagnum,* would be higher with high temperature, but we found no difference in N concentration of the *Sphagnum* capitula between the temperature treatments, except for *S. fuscum* at no N addition (Fig. 4). In another greenhouse experiment, we did find that N concentration in *Sphagnum* increased with increased temperature up to 17.2°C, but here too there were no differences in N concentration between the two highest temperatures of 17.2 and 20.6°C (Breeuwer et al. 2008a). We suspect that all the available N from the peat in the containers was mineralised in both temperature treatments during the experiment. Unfortunately, as we did not monitor N concentration in the *Sphagnum* material during the experiment, we could not follow the response curve of N concentration to temperature over time to verify this.

Nitrogen

Our last hypothesis was confirmed: increased N concentration had a negative effect on height increment and production of all *Sphagnum* species; this was especially evident in the second year of the experiment. Atmospheric N deposition in Europe varies from 0.1 to 2 g N m^{-2} $year^{-1}$ (Bragazza et al. 2004), although higher values up to 5 g N m^{-2} $year^{-1}$ are reported for the Netherlands (RIVM 2004). Our N addition of 4 g N m^{-2} $year^{-1}$ is therefore already relatively high, but actual N availability might have been even higher because of nutrient mineralisation from the *Sphagnum* and peat in containers. The high N concentrations we found were roughly equal to the maximum N concentration in *Sphagnum* of 20 mg g^{-1} estimated by Berendse et al. (2001). Nitrogen concentrations were higher in the high N treatment: the N concentrations of *S. fuscum* and *S. magellanicum* in particular increased compared to initial values. Hummock species are known for their high N uptake rate (Jauhiainen et al. 1998). In another greenhouse experiment we performed, N concentrations were also higher in *S. fuscum* and *S. magellanicum* than in *S. balticum* and *S. cuspidatum* (Breeuwer et al. 2008a).

The negative effect of the high N treatment on height increment in all combinations is probably mainly the result of direct toxic effects of the high N concentration on *Sphagnum*, as found in other studies with N deposition above 4 g N m^{-2} $year^{-1}$ (Gunnarsson and Rydin 2000; Limpens and Berendse 2003a; Nordin and Gunnarsson 2000). As the N:P ratios were already relatively high at the start of our experiment, with values of 25 or higher, this might indicate that *Sphagnum* was already P limited, since P limitation occurs at high N:P ratios (>15 according to Aerts et al. 1992; >30 according to Bragazza et al. 2004). Bragazza et al. (2004) suggest that the critical load of N deposition in Europe is 1 g N m^{-2} $year^{-1}$, above which *Sphagnum* plants change from being N-limited to being P and K co-limited at N:P > 30 and N:K > 3. This would indicate that *Sphagnum* was P-limited in all treatments in our study and co-limited by P and K in the high N treatment. Similar effects were reported by Gerdol et al. (2007) who found that *Sphagnum* production was slightly depressed with N addition of 3 g N m^{-2} $year^{-1}$ but no concomitant addition of P; nutrient imbalance in the tissues was presumably responsible for this finding. Production in containers with the southern species was affected most by high N addition, but this was not reflected in the N concentrations or N:P and N:K ratios. Perhaps, these species were more sensitive to high N concentrations.

Another possible explanation for the negative effect of high N addition, especially in the second year of the experiment, could be decreased *Sphagnum* vitality in the containers that suffered from severe fungal infection. The percentage *Sphagnum* affected by fungal infection also rose in the second year of the experiment, particularly in the 'wet' species. As a result, the cover of dry species increased (Fig. 2). The percentage dead *Sphagnum* as a result of this infection was higher in the high N treatment (Fig. 5). Limpens et al. (2003) also found that a high capitulum N concentration increases fungus-induced necrosis in *Sphagnum.* No such relationship was found in our study, but the *Sphagnum* in our study seemed to suffer more from the fungal infection, not only bleaching and defoliating, but also disintegrating, so probably plant cells were broken down and N was no longer retained in the infected plants.

Implications of global change

Our findings suggest that the production of *Sphagnum* species is negatively affected by an increase in N deposition as well as by an increase in temperature. Decomposition is expected to increase with increased temperature and N deposition (Bragazza et al. 2006; Hobbie 1996; Mack et al. 2004), which would mean that global change can reduce the carbon storage capacity of bogs. However, the negative impact from global change might be mitigated to some extent as not all species seem to react equally strongly to increased temperature and nitrogen availability. In this study, the 'dry' species seemed to suffer less from high N and increased in cover with increased temperature. This is an encouraging outcome because some studies have estimated higher carbon sequestration in lawns and low hummocks than in hollows, although this also depends on climatic factors like temperature and moisture availability (Belyea and Clymo 2001; Laine et al. 2007). On the other hand, a large amount of carbon is sequestered in northern species, and we found that compared with southern species, their production decreased more as a result of increased temperature. We conclude that it is difficult to produce quantitative estimates of the effects of global change on the carbon storage capacity of bogs, based solely on the response of the *Sphagnum* vegetation to increased temperature and N availability. Models that simulate climate change in peat bogs should also consider the possible effects of water availability and the effects on and interactions with the vascular plant vegetation (Heijmans et al. 2008).

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